INTRODUCTION

The presence of complex pericellular baskets (nests) around the bodies of pyramidal neurons of the human motor cortex of newborns and young infants was first described by Cajal in 1899. He suggested that possibly two different types of fibers may enter into the formation of these baskets. He pointed out, on the one hand, that thin fibers representing the axonic collaterals of stellate cells of layers III and V are found terminating in the baskets, and on the other hand, that thicker fibers also seem to terminate in the baskets. He considered these thick fibers to be afferent ones, and recorded this idea in one of his drawings (see Fig. 362 of Cajal's book) in which a fiber 'a' entering a basket is labeled as an afferent fiber. Of these two possibilities, the formation of pericellular baskets of the human motor cortex by the axons of interneurons has been recently confirmed.

The morphological characteristics of a special type of stellate interneuron, 'the cortical basket cells', have been analyzed and described elsewhere. These neurons have long horizontal and vertical dendrites and an axon which branches into several long horizontal collaterals. From these collaterals, the terminal fibrillae which enter into the formation of the baskets originate. The basket cells can be found within the motor cortex from layer II to lower layer V. Pericellular baskets derived from these interneurons are formed progressively around all the pyramidal cells of those cortical layers during the course of cortical ontogenesis. The appearance and the maturation of the cortical basket cells (and hence of the pericellular baskets) follow that of the pyramidal neurons of the different cortical layers with which they establish contacts. Both of these neurons maintain a close structural interrelationship and together constitute basket-pyramidal subsystems composed of various horizontal strata. These subsystems as well as the axons of the basket cells are distributed within vertical planes perpendicular to the long axis of the precentral gyrus. It was concluded from these studies that the human motor cortex can be considered to be...
subdivided into a series of parallel vertical basket-pyramidal subsystems, arranged in several horizontal strata, which are perpendicular to the long axis of the precentral gyrus. These vertical subsystems are reminiscent of the functional vertical 'columns' or 'walls' described in the somesthetic and visual cortices of the cat and the visual cortex of the monkey.

While the second possibility suggested by Cajal, namely that afferent fibers may also enter into the formation of the pericellular baskets of the human motor cortex was not confirmed in the above-mentioned studies, it was not ruled out. The present communication reports additional observations which confirm that the pericellular baskets of the human motor cortex are indeed formed also by a special type of afferent fiber. The morphological characteristics, the distribution, and the spatial orientation of these 'basket-forming' afferent fibers of the motor cortex of a 2.5-day-old infant are analyzed and discussed in this communication.

MATERIALS AND METHODS

The motor cortex (precentral gyrus — area 4) of a 2.5-day-old infant was studied. The infant died 60 h after birth in respiratory failure caused by severe micrognathia, glossoptosis and posterior cleft palate (Pierre Robin anomaly). At autopsy, performed 2 h after death, no other major malformations were found and the external configuration, weight and anatomical features of the brain were within normal limits. Eighty-four sections of the motor cortex of this infant stained by the rapid Golgi method were prepared and studied. The staining procedure has been described in detail elsewhere.

Fig 1 Details of 3 consecutive Golgi sections (A, B and C) of the motor cortex of a 2.5-day-old infant showing the rich plexus of afferent fibers of layer V and its numerous pericellular baskets. Notice the absence of stained neurons in these Golgi preparations. The plexus corresponds anatomically to layer V of the motor cortex. The plexus also coincides in location with the internal band of Baillarger. The pericellular baskets of these Golgi sections appear as complex concentrations of fibrillae easily identified from the rest of the fibers of the plexus by their roughly pyramidal configuration. Section A illustrates the heavy concentration of pericellular baskets occasionally encountered in some areas of the plexus. This concentration of afferent fibers and pericellular baskets makes it possible to see the plexus in these Golgi preparations with the naked eye. In this section a basket-forming afferent fiber is marked by an arrow. Camera lucida drawings of two additional afferent fibers encountered in this section are reproduced in Fig 2A. Section B illustrates another less compact area of the plexus of layer V and its pericellular baskets. A long horizontal collateral (arrows) of one of the afferent fibers with pericellular baskets formed above and below it is illustrated in this section. This particular horizontal collateral and its original afferent fiber is reproduced (camera lucida drawing) in its entirety in Fig 2B (fiber a). Camera lucida drawings of two additional basket-forming afferent fibers encountered in this section are also reproduced in Fig 2B. Section C illustrates in higher magnification several pericellular baskets (a–f) showing their pyramidal configuration and complex structural organization. Some of these baskets (a, d and e) are more completely formed than others (b, c and f). Camera lucida drawings of two basket-forming afferent fibers encountered in this Golgi section are reproduced in Fig 2C. Insert D illustrates a closer view of the pericellular basket a of section C. This pericellular basket has been photographed at a different depth from that used in section C to demonstrate its apparently empty central cavity which is occupied by the unimpregnated body of the pyramidal neuron it envelopes. Motor cortex of a 2.5-day-old infant. Rapid Golgi method. Scale = 100 μm.
**Observations**

Due to one of those unexplainable staining behavior characteristics of the rapid Golgi method, no neurons were stained between cortical depths ranging from 1000 to 1400 \( \mu \text{m} \) from the pial surface in 6 consecutive sections of the 84 prepared of the motor cortex of this infant (Fig 1). Although no neurons were stained between these cortical depths a rich plexus of horizontal fibers was instead beautifully stained at that level and within it numerous pericellular baskets were found (Fig 1). At the time of birth, the region of the motor cortex located between cortical depths ranging from 1000 to 1400 \( \mu \text{m} \) from the pial surface corresponds to layer V. The 6 consecutive sections under study represent a block of the motor cortex cut vertically to the pial surface and perpendicularly to the long axis of the gyrus which measures 1200 \( \mu \text{m} \) in thickness (the average thickness of a Golgi section is approximately 200 \( \mu \text{m} \)).

The area of the cortex in which the plexus is clearly visible, because of the fortuitous absence of stained neurons, measures 3000 \( \mu \text{m} \) in width on each one of the 6 consecutive sections. The plexus of horizontal fibers of layer V of the motor cortex of this infant occupies therefore an area 1200 \( \mu \text{m} \) thick, 3000 \( \mu \text{m} \) wide, and 400 \( \mu \text{m} \) high, and it is located between 1000 and 1400 \( \mu \text{m} \) from the pial surface.

*The plexus* The plexus (Fig 1) is largely composed of horizontal fibers and occupies the territory of layer V of the motor cortex. It is clearly outlined and visible in these Golgi sections even to the naked eye. Grossly, it appears as a thick fibrous band parallel to the pial surface which follows the normal surface contour of the gyrus. Anatomically it corresponds in cortical location to the internal band of Bauldoff. Microscopically, the plexus is composed of predominantly thick long horizontal and oblique fibers with numerous pericellular baskets among them (Fig 1).
horizontal fibers run largely parallel to the pial surface and perpendicular to the long axis of the precentral gyrus (Figs 1 and 2). A single horizontal fiber of the plexus can be followed for a long distance (up to 1000 μm) within the same plane showing very little deviation in depth (from 25 to 75 μm) within the section (Figs 1B and 2B, fiber a). The plexus has also oblique fibers, which are less numerous than the horizontal ones and are also distributed within vertical planes perpendicular to the axis of the gyrus. From the horizontal and oblique fibers of the plexus numerous ascending, descending and oblique fine fibrillae originate. These fine fibrillae enter in the formation of the pericellular baskets (Fig 2). After a short course the fibrillae become transformed into peculiar structures with fusiform dilatations and terminal club-like prolongations (Fig 2) which represent portions of the wall of the baskets formed by them.

The pericellular basket. The pericellular baskets (Fig 1) are complex structures composed of fine fibrillae arranged around the body and the first portion of the dendrites and axon of the giant pyramidal cells of the motor cortex. The configuration of the basket resembles that of the body of the neuron it surrounds (Fig 1C and D). The most common type of basket observed in these Golgi preparations are the pyramidal-shaped ones (Fig 1D). The fibrillae of the basket have many fusiform dilatations and club-like terminal projections which are believed to represent axo-somatic contacts between the fibrilla and the body of the neuron. Each fibrilla of a basket seems to go around the neuronal body for a considerable distance in order to establish a relatively few number of contacts. It appears as if the body of the pyramidal neurons was covered by a fenestrated thin envelope (probably glial) compelling the fibrilla to go around in order to find the opening through which it can establish axo-somatic contacts. This fact could explain the considerable overlaps among the fibrillae of a basket, its larger size when compared with that of the neuronal body it envelops and its complex structural organization.

The fibrillae upon approaching the neuronal body resolve into a skein-like structure around it. These fibrillae arrive from the different horizontal collaterals of a single afferent fiber or from the collaterals of different fibers. In either case all the horizontal collaterals which enter into the formation of a basket belong to the same vertical plane. A single fibrilla can participate in the formation of several baskets within the same plane and each basket is formed by many fibrillae. The pericellular baskets described here are morphologically identical to those formed by the axonic collaterals of the cortical basket cells previously described. The structural characteristics, the thickness, the fusiform dilatations, and the terminal club-like projections of the fibrillae derived from either the cortical basket cell axons or the fibers described here are morphologically identical and undistinguishable in Golgi preparations.

The basket-forming afferent fiber. Several thick ascending fibers are seen entering and branching within the plexus of layer V of the motor cortex of this infant (Figs 1 and 2). These fibers appear abruptly within the thickness of the section as if they were formed 'de novo' at the point of their appearance. They are considered to be myelinated afferent fibers up to the proximity of layer V of the motor cortex (Fig 2A-C). Upon arriving at the vicinity of layer V they seem to lose their myelin covering.
and hence become susceptible to the silver impregnation of the Golgi method. In Golgi preparations they become visible abruptly within the thickness of the sections since their myelin covered portions are not visible in these preparations. These fibers are thick and prominent and after a short ascending course they branch within layer V into predominantly long horizontal and oblique collaterals (Fig 2A–C). All the collaterals from a single afferent fiber seem to be distributed within the same plane and they show little deviation in depth within the section.

The territory of distribution of a single basket-forming afferent fiber becomes determined by a narrow vertical plane which is perpendicular to the long axis of the precentral gyrus. This vertical plane may measure up to 1000 μm in length, 400 μm in height and only 25–75 μm in width. It is located within the territory of layer V and is composed of several horizontal strata represented by the horizontal collaterals of the fiber. All the giant pyramidal neurons contacted by a basket-forming afferent fiber belong to the same anatomical plane of the fiber and possibly to the same functional ‘column’ or ‘wall’. The territory of distribution of these afferent fibers at the time of this observation (2.5-day-old infant) seems to be mainly restricted to layer V of the motor cortex. However, there are indications suggesting a larger territory of distribution for these fibers involving also the lower region of layer III. Some of these afferent fibers (Fig 2A–C) already show, at this age, ascending prolongations approaching the lower region of layer III. In addition, many of the horizontal collaterals of these afferent fibers show fine terminal prolongations suggesting growing fiber tips. Therefore, at this age, these basket-forming afferent fibers are considered to be actively growing and their final territory of distribution should be larger than the one here described. However, there are no indications in this study suggesting that any further development of these fibers would be other than within the spatially oriented planes already established by them at this age. Furthermore, neither are there indications to suggest any change in the nature (formation of pericellular baskets around the bodies of pyramidal neurons) of these fibers in the course of later cortical development.

**DISCUSSION**

The present study confirms original observations made by Cajal in 1899 concerning the possible double origin of the pericellular baskets formed around the pyramidal neurons of the human motor cortex. It illustrates the structural characteristics and intracortical distribution of a special type of afferent fibers of the motor cortex of a 2.5-day-old infant. It demonstrates that in addition to their intrinsic component the pericellular baskets formed around the bodies of the giant pyramidal neurons of layer V have also an extrinsic one. The intrinsic component of the pericellular baskets originates from a special type of stellate interneuron named the cortical basket cell. The extrinsic component originates from a special type of afferent fiber, reported in this communication, named the ‘basket-forming’ afferent fibers of the human motor cortex.

The suggestion made by Cajal that the smaller basket may be formed by the
axon terminal of stellate interneurons while the larger one may be formed by the afferent fibers is not supported by the observations made in this or the previous study concerning the baskets of the human motor cortex. These studies demonstrate a double origin for the pericellular baskets formed around the bodies of the giant pyramidal neurons of layer V of the motor cortex. Furthermore, they also suggest a possible double origin for the pericellular baskets formed around the bodies of the pyramidal neurons of lower layer III. Concerning the origin of the pericellular baskets formed around the bodies of the pyramidal neurons of upper layer III and layer II of the motor cortex, so far, only an intrinsic component has been demonstrated in them. However, the possibility of the development of an extrinsic component in them during the course of late postnatal cortical development cannot be ruled out at present. The material on which these studies are based belong to newborns and young infants 2 and 2.5 months of age, and there is no available information on the motor cortex of older infants. The progressive ascending development of the motor cortex in general and of the formation of the pericellular baskets in particular during the course of prenatal and early postnatal cortical development should be kept in mind when interpreting observations made during these ages. Many of these observations represent simply developmental stages of the fibrillar-neuronal organization of the cerebral cortex and the systems to which they belong are not as yet fully established as definite ones at these ages. It is possible that the basket-forming afferent fibers of layer V, which are still growing at the time of birth, may extend into the territory of layer III and even further (layer II) in the course of late postnatal cortical development. Therefore, pericellular baskets may be formed by these fibers also around the bodies of the pyramidal neurons of the upper cortical layers. Indications of the formation by these fibers of pericellular baskets around the bodies of the pyramidal neurons of the lower region of layer III are already recognizable at the time of birth. The final territory of distribution of these fibers should be considered to be more extensive than the one here described. There are no reasons to believe that the extension of these fibers in the course of late cortical development will be outside the spatially oriented vertical systems already determined by them at the time of birth. Neither are there indications in this study to suggest any change in the nature of these basket-forming afferent fibers in the course of cortical development.

The intracortical distribution and spatial orientation of the basket-forming afferent fibers should be emphasized as it probably relates to their function. These fibers are distributed within narrow vertical planes which are perpendicular to the long axis of the precentral gyrus. It is of interest to recall that the cortical basket cells and their axons are similarly oriented and distributed within the motor cortex. This observation suggests that both the basket-forming afferent fibers (extrinsic component) and the cortical basket cells (intrinsic component) are structurally, spatially and probably functionally interrelated within the motor cortex. Both have developed a similar type of terminal contact with the bodies of the pyramidal neurons and are similarly distributed and oriented within the motor cortex and both contact selectively the pyramidal neurons located within their plane of distribution. The structural simi-
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<td>Axons of the basket cells</td>
<td>Thinner</td>
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<td>Basket-forming afferent fibers</td>
<td>Thicker</td>
<td>Always ascending</td>
<td>Long, thick, horizontal and oblique</td>
<td>Within narrow vertical planes perpendicular to long axis of the precentral gyrus</td>
<td>Formed by fine terminal fibrillae</td>
<td>Layer V at the time of birth**</td>
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* Both types of pericellular baskets are morphologically identical and are indistinguishable in Golgi preparations.

** The basket-forming afferent fibers are actively growing at the time of birth with ascending collaterals approaching the lower region of layer III suggesting a possible extension into it during the course of postnatal cortical ontogenesis.
larities and the differences between these two basket-forming systems are summarized in Table I.

The human motor cortex can then be considered to be subdivided into a series of parallel vertical planes which are reminiscent of the functional ‘walls’ described in the visual cortices of the cat and monkey. Within each of these vertical planes an intrinsic and an extrinsic subsystem of fibers activate all the pyramidal neurons in it. Such a combination of an afferent fiber and an intracortical neuron acting directly upon a large projective neuron has been described in other areas of the central nervous system and frequently these fibrillar-neuronal combinations are also spatially oriented. It is perhaps in the cerebellum and its related nuclei that the structure and function of this type of fibrillar-neuronal association has been better studied and understood. In such fibrillar-neuronal combinations the intracortical neurons are Golgi type II cells and seem to exercise a modulatory influence upon the afferent inputs.

The function of the basket-forming afferent fibers of the motor cortex described here remain unknown. A possible inhibitory function is perhaps suggested by the formation of terminal pericellular baskets (axo-somatic contacts). Similarly, an inhibitory function has been also suggested for the cortical basket cells of the motor cortex. The structural similarities among the cortical basket cells, the cerebellar basket cells and the basket cells of the hippocampus have also been pointed out. The already demonstrated inhibitory function of the last two types of neurons give further support to the assumption that the cortical basket cells of the motor cortex may be inhibitory neurons. The fact that formation of pericellular baskets around large projective neurons is a feature common to these 3 types of neurons and to the basket-forming afferent fibers, described here, suggests a possible similar functional role among them. Needless to say, neurophysiological studies are necessary to confirm the functional role of the cortical basket cells and of the basket-forming afferent fibers of the human motor cortex.

The origin of these basket-forming afferent fibers of the motor cortex is unknown at present. However, their direct contact with the giant pyramidal tract neurons of layer V, their specific terminations forming individual baskets around the bodies of those neurons, and their distinct spatial orientation within parallel narrow vertical planes makes the nucleus ventralis lateralis (VL) of the thalamus a likely origin for them. The existence of projections from the neurons of the nucleus ventralis lateralis to the motor cortex (precentral gyrus — area 4) is well known. This nucleus is considered to be a specific relay center of the cerebello-thalamo-cortical pathway. It receives afferents from the contralateral deep cerebellar nuclei and from the ipsilateral red nucleus and transmits cerebellar impulses to the motor area of the cerebral cortex. Recent retrograde degeneration studies in the cat have demonstrated localized projections to the motor cortex from the VL nucleus. Neurophysiological studies have also shown that the thalamo-cortical fibers from the neurons of the VL nucleus make direct and powerful monosynaptic connections with the large pyramidal tract neurons of the motor cortex. It seems, therefore, that some of the characteristics attributed in these studies to the thalamo-cortical connections between the VL

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neurons and the pyramidal tract neurons of the motor cortex coincide with those of the basket-forming afferent fibers of the motor cortex described in this communication. These structural similarities give some support to the postulated origin for these basket-forming afferent fibers of the human motor cortex and should encourage further exploration into their origin and functional nature.

SUMMARY

The structure, intracortical distribution and orientation of a special type of basket-forming afferent fiber from the motor cortex of a 2.5-day-old infant is presented. The existence of these fibers confirm original observations made by Cajal concerning the origin of the pericellular baskets of the human motor cortex. It is concluded from this study that the pericellular baskets formed around the bodies of the giant pyramidal neurons of layer V (and possibly of lower layer III) of the human motor cortex have a double origin from intrinsic and extrinsic sources. The intrinsic component of these pericellular baskets is furnished by a special type of stellate interneuron previously described and named the cortical basket cell. The extrinsic component is furnished by the basket-forming afferent fibers described in this communication. Both of these subsystems are similarly distributed and oriented within narrow vertical planes perpendicular to the long axis of the precentral gyrus of the motor cortex. The dimensions of the planes determined by the intracortical distribution of these two subsystems are also similar. It is suggested that there is a close anatomical and possible functional interrelationship between these two subsystems of the motor cortex. Although the origin of these basket-forming afferent fibers is unknown it is postulated that they may originate in the projective neurons of the nucleus ventralis lateralis of the thalamus and that they may be part of the cerebello-thalamo-cortical pathway.

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